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Rheotactic Responses in the Marine Mollusk *Littorina planaxis* Philippi

BY

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(4 Text figures)

INTRODUCTION

The following experiments were carried out at Hopkins Marine Station of Stanford University in 1964 during April and May, the mating season of *Littorina planaxis* (Philippi, 1847). At the end of May a population survey showed that this species was found primarily between +4 feet and +10 feet from zero tide level. The *L. planaxis* used for the experiment were taken from two populations, which were between +3 feet and +8 feet.

Most of the *Littorina planaxis* at China Point, Monterey, California, range between 6 mm and 15 mm in height. The animals used in this study were between 9.5 mm and 13.5 mm. This size is slightly larger than the littorines in the intermediate group with which North (1954) worked in his maximum current study. North (*l. c.*) reports that a current of 230 cm/sec was sufficient to dislodge a majority of snails. The currents used in the present experiments ranged from 5 cm/sec to 58 cm/sec. The temperatures of the water used for the experimental currents varied from 12.6° C to 13.2° C, which is slightly warmer than the range of the morning sea temperatures for the same period.

A POSITIVE RHEOTAXIS

The first experiment (experiment A) was performed at each of the four tidal periods. The following procedure was used: (1) A pair of snails taken from the field was allowed to attach to a glass plate; a current initially aimed at the posterior end of the shell was then introduced and the behavior recorded for about 20 minutes; (2) the same pair was placed in a glass tube, 150 cm long and 2 cm in diameter; the tube was fixed horizontally on a black background and completely filled with water, which flowed at 27 cm/sec; the horizontal and angular movement of the pair was recorded for about 30 minutes; (3) step one was then repeated, and the pair of snails was stored in the laboratory in dry collection bottles. The apparatus was cleaned after each test to prevent old mucous trails from having any effect.

Sixteen animals were tested in this manner for two consecutive tidal periods. When snails were responding to currents on the glass plate in steps 1 and 2, there were twice as many individual turns to the left as to the right. Sixty-four per cent of 55 trials were essentially as illustrated in Figure 1. The responses observed in step 1 were insignificantly different from the responses observed in step

Figure 1

Typical Response of *Littorina planaxis* on a Glass Plate. Arrow indicates the direction of the water current.

3. A control experiment was performed to see if the unnatural glass substrate was introducing any systematic error. Sand substrates of two different degrees of coarseness were used on 4 trials. The pair of snails used showed the typical response.

The behavior displayed in the flow tube was essentially uniform. Most of the snails showed a positive response regardless of initial orientation (Figure 2a). The exceptions were one female reacting entirely negatively; and three females and one male showing no response during the 30 minute test period. Of the other eleven, three showed brief negative responses. A negative geotaxis and preferences for an inverted position occurred during about 80% of the experiments (Figure 2b). Individual rates were commonly sporadic and varied from 0 cm/min to 7cm/min. The average for 30 minutes was 1.4 cm/min. No correlation between activity and sex or tidal period could be observed.

Another test lasting for an hour and a half was made on four snails. It suggested that the rate of movement might be inversely proportional to current velocities of 12 cm/sec, 36 cm/sec, and 59 cm/sec. In general, whenever the current became too great the animals would withdraw their heads. They oriented into the current unless the initial force was too great. If the current was strong the animal formed a suction grip with the foot in a preservation reaction and failed to respond rheotactically. The fact that they oriented into the current, when possible, is in agreement with NORTH's observation that *Littorina planaxis* were easier to dislodge when posteriorly oriented to the current.

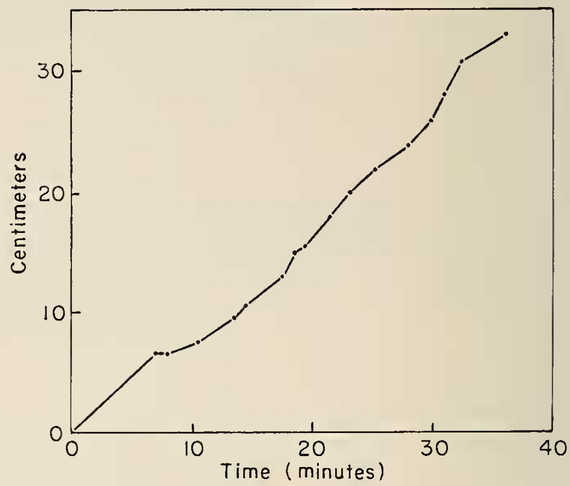


Figure 2a

Typical Horizontal movement of *Littorina planaxis* in a Glass Tube and Subjected to a Water Flow of 27 cm/sec.
Ordinate - in centimeters Abscissa - time in minutes

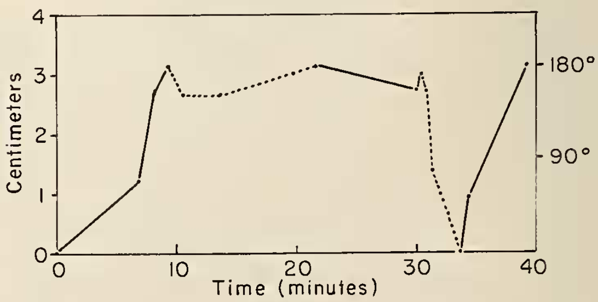


Figure 2b

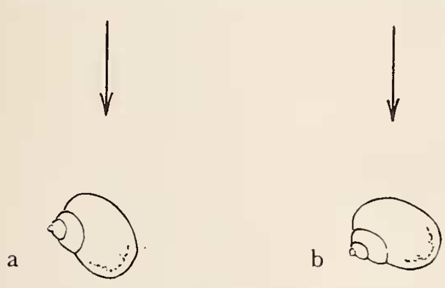
Typical Vertical Movement of *Littorina planaxis* in a Glass Tube of 2 cm Diameter and Subjected to a Water Flow of 27 cm/sec.
Ordinate - in centimeters Abscissa - time in minutes
Solid line indicates movement through the 180° of the left half of the tube when looking into the flow; dotted line indicates movement through the 180° of the right half of the tube.

The positive rheotaxis appears to be a strong response. In one experiment begun on six *Littorina planaxis,* one animal demonstrated a strong positive taxis after seven days of a continuous current flowing at 36 cm/sec. Over half, however, either crawled out or were washed out of the tube after 48 hours.

In repeating experiment A a month later on the snails first used, several behavioral tendencies seemed more stereotyped. Because of the weakened condition of the starved animals, only half the current first used was employed. Even then, activity was appreciably decreased. Stops were more frequent and angular movement dropped to almost zero except in the cases of the negative geotaxis and inversion, which occurred only 50% of the time. There were, however, no negative rheotactic responses, and the ratio of left to right turns, observed during steps 1 and 3, increased from 2:1 to about 5:1. The direction of the flow was reversed for half of the tests to act as a control for possible systematic error.

There appears to be an innate tendency for counter-clockwise movement in *Littorina planaxis.* On several occasions in steps 1 and 3 of experiment A snails, which were allowed to attach, spontaneously started to turn to the left. As the plates were damp, perhaps part of *L. planaxis's* behavior is a kinesis instead of a taxis. Four snails with tentacles removed and one pair with only the right tentacles removed exhibited the typical responses in experiment A. A population study was made in the field on 339 large (12 mm - 16 mm) *L. planaxis* located on a vertical rock surface at +12 feet to +22 feet. Forty-seven per cent were oriented vertically and 44% were oriented from 5° to 85° to the left of the vertical.

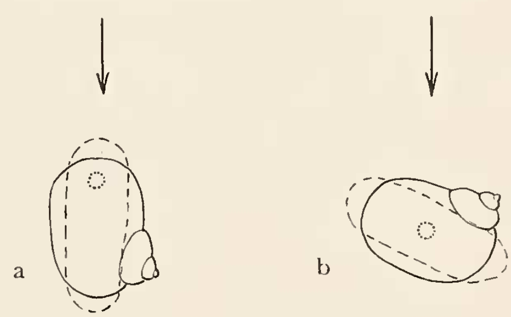
The asymmetrical periwinkle shell and its hydrodynamic



Figures 3 a and 3 b

Top View of the Final Orientation of *Littorina planaxis* Shell in a Water Current. The current is greater in a than in b. The arrows indicate the direction of the current.

properties are of importance in influencing the behavior of the snails. Two types of experiments were attempted in order to determine the physical effects of water currents on the shell alone. In the first, a withdrawn *Littorina planaxis* was repeatedly placed in a current at various angles from the currential axis. Regardless of the initial orientation, the forces oriented the shell negatively. Directly depending upon the current rate, an angle from 75° to 30° to the left of the current axis was formed (Figures 3 a and 3 b). In the second experiment, unoccupied shells of 14 mm height were mounted on small rods attached at various positions in the area which the extended foot would normally occupy. If the attachment was in the anterior region, as would be the case when the foot first protrudes, the shell oriented directly into the current. If the attachment was more posterior, which would correspond to the center of the attachment forces of a fully extended foot, the shell oriented to the left, exposing its right side (Figures 4 a and 4 b). Thus, it would be easier



Figures 4 a and 4 b

Top View of the Final Orientation of an Unoccupied *Littorina planaxis* Shell Supported by a Wire Rod in a Water Current. Dotted circles indicate the points of attachment. The cross-hatched areas represent the area which the extended foot of an occupied shell would cover.

for a *L. planaxis* to make a left turn when either the tail or right side of its shell were facing the current; and easier for a right turn to be made when the left side was perpendicular to the current because these are the same directions in which the shell alone is forced by water currents. Perhaps the physical properties of the shell have conditioned *L. planaxis* to counter-clockwise movement.

GEOTAXIS versus RHEOTAXIS

Tests which were allowed to continue overnight on 50 snails, and tests, which lasted for one hour, on 24 snails indicated that a negative geotaxis dominates the positive rheotaxis. This holds for angles of 8°, 10°, 15°, 30°, 45°, and 90° from the horizontal with a current of 25cm/sec. The rates of movement suggest that it might be more difficult for the snail to exhibit a negative geotaxis when traveling with the current. This is to be expected when one recalls the fact that the snails were easier to dislodge when currents were directed at the posterior end of the shell. Thus, the snail probably has to put more energy into its efforts to remain attached to the surface.

PHOTOTAXIS versus RHEOTAXIS

Tests on 20 snails in tubes of still water suggest that *Littorina planaxis* is positively phototactic when completely submerged, in an inverted position, and in a light gradient. It often takes several hours to elicit a total response in the population. Nevertheless, a current of 5 cm/sec drew 30% of the population away from the lighted end in 45 minutes and 70% of the population in three hours.

General illumination seemed to have no appreciable effect on the experiments, although changes in intensity initially evoked a tentacle withdrawing response.

DISCUSSION

Like *Nerita japonica* Dunker, 1859[1], *Tegula funebralis* (A. Adams, 1855)[2], and others, *Littorina planaxis* appears to be positively rheotactic. Unlike *T. funebralis,* this response does not seem to change in time. In addition to the physiological advantages of having the mantle cavity receive the maximum current, which would result from counter-clockwise movement and a positive rheotaxis, perhaps there is a selective value in a positive rheotaxis due to the physical nature of breaking waves and their withdrawing currents.

Studies so far suggest that *Littorina planaxis* would respond to a combination of taxes as *Littorina neritoides* Linnaeus, 1758[3] does.

Similar rheotactic and geotactic experiments begun on *Littorina scutulata* (Gould, 1849) failed to reveal any differences in responses.

[1] see Suzuki, 1935

[2] see Overholser, 1964

[3] see Fraenkel & Gunn, 1940, p. 299, fig. 135

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